



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE COSTA RICAN SPECIES OF EPIGOMPHUS AND THEIR MUTUAL MATING ADAPTATIONS

(ODONATA)

BY PHILIP P. CALVERT

University of Pennsylvania, Philadelphia, Pa.

(With Plates XIII, XIV and XV)

Abstract

This paper increases the number of Costa Rican species of *Epigomphus* from five to seven and adds data on distribution, colors and structure of all of them.

Adds data on the variation of the generic characters.

Announces a hitherto undetected secondary sexual character in the tarsus of the third leg of the males, which is also a new generic character.

Makes known one hitherto unknown species (*E. subsimilis*) and the previously undescribed female of one other species (*E. tumefactus*).

Attempts a correlation of the form of the heads of the females and the male abdominal appendages as concerned in the act of mating and figures the heads of the females more fully than ever before.

Contents

	Page
Historical Introduction.....	323
Distribution of <i>Epigomphus</i> in Costa Rica.....	325
Generic Characters of <i>Epigomphus</i>	327
Synopsis of the Species and Notes on their Colors, Vulvar laminae, etc.	331
Mutual Mating Adaptations.....	338
Explanation of Plates.....	353

HISTORICAL INTRODUCTION

The "sous-genre *Epigomphus* Hagen" was first published by de Selys in 1854 in the *Synopsis des Gomphines*, one of those joint works by the Belgian and the Prussian writers in which it is often

difficult to exactly define the authorship of certain taxonomic groups according to the strict letter of codes of nomenclature. *Epigomphus* was established for a single species, *paludosus* Hagen, from Brazil. To it de Selys added, in 1869, *obtusus* from São Paulo on the upper Amazon and Pebá, and, in 1878, *subobtusus* from the volcano Irazú, Costa Rica, and San Agostino, Guatemala.

In 1903¹ the present writer discussed this genus, adding the new species *llama* from Chulumani in Bolivia, *quadracies* from San Isidro in Guatemala and Chiriqui, Panama, and *tumefactus* from Cachí, Costa Rica, giving a synopsis of the six known species and references to the previous literature. As much of this synopsis and references as concerned the Central American species was reproduced in the *Biologia Centrali-Americana*² in 1905, including a previously unknown species, *camelus*, from Carrillo, Costa Rica. Still another species, *verticicornis*, from Tuis, Costa Rica, received as the *Biologia* volume was being completed, found a place on the last page of the text.³

In an extensive and important work, *Libellen (Odonata) aus der Region der amerikanischen Kordilleren von Costarica bis Catamarca*⁴ Dr. F. Ris has dealt with *Epigomphus*, giving a table of the males of six species in which the new species *armatus* from Finca Hundriesser, Costa Rica, and *hylaesus* from Matto Grosso, Brazil, are included.⁵

The writer's personal collecting in Costa Rica in 1909-10⁶ and specimens subsequently gathered in that country by Messrs. C. H. Lankester and D. E. Harrower and sent to him bring the total of Costa Rican species of *Epigomphus* to seven.

¹Entomological News, xiv, pp. 184, 186-191.

²Volume Neuroptera, pp. 169-172.

³*T. c.*, p. 410, 1908.

⁴Archiv für Naturgeschichte, 82 Jahrgang 1916, Abteilung A, 9 Heft. Ausgegeben im Juli 1918. Berlin. pp. 1-197. 117 figures in the text and on two double plates.

⁵*T. c.*, pp. 145-154.

⁶See A Year of Costa Rican Natural History by Amelia S. and Philip P. Calvert. New York. The Macmillan Co., 1917.

DISTRIBUTION OF *EPIGOMPHUS* IN COSTA RICA

The species of *Epigomphus* known to me as occurring in Costa Rica follow. The specimens here recorded for the first time are listed in full; data previously published in the *Biologia* volume and by Dr. Ris are briefly cited. Unless otherwise stated the new material is in the writer's collection and a first set will be placed in the collection of The Academy of Natural Sciences of Philadelphia.

1. *E. camelus* Calvert

Juan Viñas, 3400 feet (1036 meters), June 24, 1909, one ♂, taken on rock along stream issuing from foot of nearer waterfall;⁷ 3900 feet (1188 meters), June 29, 1909, two ♂, at small streams, along the edge of the cañon where sugar cane fields and forest meet, Calvert.

Carrillo, ca. 300 metres (*Biologia*).

2. *E. subsimilis* new species

Turrúcares, 2200 feet (670 meters), August 14 and 15, 1909, in maize and banana field ("platanal") near left bank of Rio Siquiares, all in the afternoon, three ♂, five ♀ (dry), one ♂, two ♀ (in alcohol), Calvert.

3. *E. quadracies* Calvert

Rio Chirripo, July 19, 1 ♂; July 25, 1 ♀; July 26, 1 ♂, 1 ♀; all taken in 1915, by D. E. Harrower.

Alajuela, ca. 3200 feet (975 meters), August 4, 1 ♂, 1 ♀; August 8, 2 ♀; all taken in 1915, by D. E. Harrower.

This species, originally described from Guatemala and Panama, has not been recorded previously from Costa Rica. I have also before me a male from Alajuela, Panama, April 5, 1911, taken by August Busck, in the United States National Museum collection.

4. *E. tumefactus* Calvert

Estrella, April 13, 1 ♀ and April 19, 1 ♂, both in 1916, taken by C. H. Lankester.

Guapiles, Florida road west of the settlement, in the forest, 980 feet, (300 meters), June 3, 1909, 1 ♂, 1 ♀, in shady places along trail, Calvert; June 4, 1909, 1 ♂ taken by Messrs. Schaus and Barnes.

Guacimo, ca. 650 feet (200 meters), June 6, 1909, 1 ♀, in forest, Calvert.

Peralta, ca. 1050 feet (350 meters), August 7, 1909, 1 ♂, forest by brook; August 8, 1909, 1 ♂, road through woods; Calvert.

⁷Descriptions of localities at which we collected are given in "A Year of Costa Rican Natural History," and in these TRANSACTIONS, XL, pp. 1-8, 1914.

I have also a female taken by the late Professor P. Biolley, but without precise locality.

Recorded from Cachí, 3280 feet (1000 m.) and Carrillo, ca. 300 m., in the *Biologia*, and by Dr. Ris from Infernillo, Reventazon [= Juan Viñas], 1000 m., 1913.

5. *E. verticicornis* Calvert

Tuis, 2460 feet (750 meters), June, 1907, 1 ♂, 1 ♀, taken by C. H. Lankester. (These are the type and allotype described in the *Biologia* and now in the collection of The Academy of Natural Sciences of Philadelphia).

In August, 1909, I noted one female of this species from Tuis, taken by Lankester, in the Museo Nacional at San José, Costa Rica.

6. *E. subobtusus* Selys

Juan Viñas, near the Rio Reventazon, 2500 feet (760 meters), June 28, 1909 1 ♂, 1 ♀, Calvert.

Quebrada Honda, ca. 3450 feet (1050 m.), August 1, 1909, Calvert.

Mountains south of Aguacaliente, ca. 4500 feet (1370 m.), May 20, 1909, 1 ♀, in narrow lane in low woods (second growth, scrub), resting on shrub; Calvert.

Tuis, 2460 feet (750 m.), June 1907, 1 ♂, taken by C. H. Lankester (Acad. Nat. Sci., Phila.).

Recorded from Irazú and Cachí, 3280 feet (1000 m.) in the *Biologia*, and by Dr. Ris from "Tuis, Turrialba 1000 m., 1913; Orosi, Irazu 1500 m. V, 1912."

7. *E. armatus* Ris

Guapiles, Florida road west of the town, in the forest, June 3, 1909, 1 ♀, Calvert; June 5, 1909, 1 ♀ taken by Messrs. Schaus and Barnes.

Described by Dr. Ris from "Costarica: 2 ♂, 1 ♂ (das ♀ 'Finca Hundriesser')."

Dr. Ris remarks: "Gestalt und Färbung der sehr eigenartigen in dieser Gattung vereinigten Formen lässt in ihnen Walddiere vermuten und die Herkunft des immerhin noch spärlichen Materials spricht im selben Sinne."⁸ My own observations fully bear out this conjecture, although individuals and species may occur in the thin woodlands along water courses, as in *E. subsimilis* at Turrúcares.

From the preceding list of localities it will be seen that five of the seven Costa Rican species have thus far been found only on the moister Atlantic slope of that country with its more extensive forests; one species (*subsimilis*) is at present known only from the Pacific side and one species (*quadracies*) from both slopes. Too much weight must not be laid upon these statements until they have been tested by more thorough collecting.

⁸Archiv f. Naturgesch., 82 Jahrg., Abteil. A, 9 Heft, p. 145. 1918.

As to altitude *tumefactus* has been taken from nearly sea-level up to 1000 meters; *subobtusus* from 750 to 1370 meters; *quadracies* from near sea-level to 975 meters. Of the other species we have much fewer data.

As to seasonal occurrence it will be noted that all dates of capture of adults fall between April 13 and August 15, that is at the beginning, and in the first half, of the rainy season, although the Atlantic slope of Costa Rica is notoriously wetter throughout the year than the Pacific side. I believe that the absence of dates of collection within the other months has some real significance, since I personally collected at various times in the year at a number of the exact localities in which I took *Epigomphus* and did not find this genus except as recorded above.⁹

GENERIC CHARACTERS OF EPIGOMPHUS

In 1903¹⁰ I gave figures showing the percentage variation in the generic characters of this genus. Those figures were based on twenty-six individuals, viz: *E. paludosus* 2 ♂; *E. llama* 9 ♂, 5 ♀; *E. quadracies* 2 ♂, 1 ♀; *E. tumefactus* 2 ♂; *E. subobtusus* 4 ♂, 1 ♀. The present material consisting of forty-six individuals has also been examined for variations in the generic characters, and the data thus obtained have been combined with those of 1903, so that the following results are based on seventy-two individuals, except where otherwise stated. The forty-six specimens of the present material comprise *E. quadracies* 4 ♂, 5 ♀; *E. tumefactus* 5 ♂ 4 ♀; *E. subobtusus* 5 ♂, 5 ♀; *E. subsimilis* 4 ♂, 7 ♀; *E. armatus* 2 ♀; *E. camelus* 3 ♂; *E. verticicornis* 1 ♂, 1 ♀.

The generic characters are given as nearly as possibly in the same order as that in which they are listed in the *Biologia Centrali-Americana*.¹¹

No variations have been found in the following characters:

Internal (subtriangle) and discoidal triangles of the front wings free (*i. e.*, with no cross-veins).

No anal loop on the hind wings.

⁹See my itinerary in Appendix I of "A Year of Costa Rican Natural History," by A. S. and P. P. Calvert, New York, The Macmillan Co., 1917.

¹⁰Entom. News, xiv, pp. 186-187.

¹¹Vol. Neuropt., pp. 146-148.

Third femora reaching but little farther back than the first abdominal segment, armed with spines shorter than the thickness of the femur.

Front wings with M_4 (short sector) and $Cu1$ (first sector of the triangle) divergent, with ten to seventeen marginal cells between them; proximal angle of the discoidal triangle as far (or farther) distad from the arculus as (or than) the length of the proximal side of the internal triangle.

All wings without a brace-vein at the proximal end of the pterostigma.

Arculus of the front wings distal to the second antenodal at least of the subcostal series.

Cubito-anal cross-veins, including the anal crossing (submedian cross-veins), on the front wings two or more.

Males with the abdomen widest at segment ten, except in *E. llama* where segments eight to ten are equally wide; third femora with more numerous shorter spines on the flexor surface than in the female (cf. Plate XIV, figs. 11 and 12); third tibiae and first two joints of third tarsi with the spines of the antero-inferior (outer) row much shorter than those of the postero-inferior row and blunt at tip (cf. Pl. XIV, figs. 14, 19); no anal triangle.

Females with the auricles on abdominal segment two, well developed; third tibiae and third tarsi with the two rows of spines similar, slender, acute (cf.¹² Pl. XIV, figs. 13, 18).

Variations have been noted in the following characters:

Internal triangle of the hind wings free 99.31 %, with one cross-vein (1 wing) .69 %.

Discoidal triangle of the hind wings free 97.92 %, with one cross-vein (1 wing) .69 %, with two cross-veins (2 wings) 1.39 %.

Supratrangular cross-veins on the front wings absent 92.37 %, one (11 wings) 7.63 %; on the hind wings absent 97.92 % one (3 wings) 2.08 %.

Sectors of the arculus on the front wings separated by an interval less than the thickness of either sector 97.92 %, on the hind wings the same; with no interval between them, *i. e.*, contiguous (two front and two hind wings), 1.39 % each; with interval between them greater than the thickness of either sector (1 front, 1 hind wing) .69 % each.

Basal subcostal cross-veins on the front wings one 97.92 %, two (three wings) 2.08 %;¹³ on the hind wings one 96.53 %, two (two wings) 1.39 %, absent (three wings) 2.08 %.

¹²The statements for the third tarsi of males and of females are based on the present material, *E. paludosus* 1 ♂, *E. llama* 4 ♂ 3 ♀. The shorter spines of the antero-inferior row of the tibia and tarsus of *llama* ♂ are suddenly contracted near their tips into acute apices much as shown in Ent. News, xiv. pl. viii. fig. 11 for *subobtusius*.

¹³What may be described as a basal costal cross-vein exists on both front wings of a female of *E. subsimilis*; it is an *unthickened* antenodal proximal to the normal thickened first antenodal, not continuous with any cross-vein in the subcostal space but slightly distal to the level of the normal subcostal cross-vein.

Front wings with one row of cells in the anal space (postcostal cells) from base to level of the discoidal triangle 91.67 %, with two rows (two wings) 1.39 %, with some double cells but not forming two rows (ten wings) 6.94 %; with two rows of cells between *Cu*2 (second or lower sector of the triangle) and the hind margin 86.81 %, with three or more rows (nineteen wings) 13.19 %.

Arculus of the hind wings distal to the second antenodal, at least of the subcostal series, 98.61 %; at or proximal to the second antenodal, etc., (two wings) 1.39 %.

Distal thickened costal antenodal on the front wings the sixth or more remote 96.53 %, the fifth (five wings) 3.47 %; on the hind wings the sixth or more remote 94.45 %, the fifth (eight wings) 5.55 %.

Cubito-anal cross-veins, including the anal crossing, (submedian cross-veins) on the hind wings two or more 97.22 %, one only (four wings) 2.78 %.

Posttriangular rows distad to as far as the level of separation of *M*1+2 and the bridge of *Rs* (principal and subnodal sectors) on the front wings two 95.14 %¹⁴, one (seven wings) 4.86 %; on the hind wings two 99.31 %¹⁵, one .69 %.

Inferior angle of the ocellar triangle about 90° 95.83 % (or less?), about 100°-105° 4.17 % (or more?).

De Selys first called attention¹⁶ to the difference in the armature of the femora of the two sexes of *Epigomphus*: "les fémurs des mâles ne sont pas épineux, mais simplement denticulés. Chez les femelles les épines sont nombreuses et courtes." The difference is more marked between the *third* femora of the two sexes, as first and second femora of the female approach those of the male.

In 1903¹⁷ the difference in the third tibiae of the two sexes was first published.

In the present paper the further difference in the first and second joints of the third *tarsi* is pointed out and figured. It is curious that it has required forty-seven years to detect these three secondary sexual characters of this pair of legs.

¹⁴Of the one-hundred and thirty-seven wings making up this item, four (= 2.78 % of the total) have a single cell reaching across the whole width of this area.

¹⁵Of the one-hundred and forty-three wings making up this item, two (= 1.39 % of the total) have a single cell reaching across the whole width of this area.

¹⁶Bull. Acad. Roy. Belg. (2) xxxv, p. 755, or Troisièmes Addit. Syn. Gomph. p. 27. 1873.

¹⁷Entom. News xiv, p. 187.

Mention may be made here also of two abnormalities noted in the wings of the present forty-six individuals: no true pterostigma exists in the left front wing of the female of *E. tumefactus* from Guacimo; an incomplete curved cross-vein exists in the basal cell *R+M* in the left hind wing of the male of *E. quadracies* from Rio Chirripo, of July 19, 1915.

The genitalia of the second abdominal segment of the male of *E. subsimilis* are shown in Pl. XIII, fig. 4. I have expanded these organs in *subobtusus* 1 ♂, *tumefactus* 2 ♂, *quadracies* 1 ♂, *verticicornis* 1 ♂, and *camelus* 1 ♂, and compared them with those of *subsimilis* and have found no differences other than in the size of the first hamule. The form of these organs, therefore, may be considered as a generic character.

There is little difference also in the vulvar laminae of the females as they resemble that of *E. llama* of Bolivia¹⁸, but with the interval between the lobes triangular rather than quadrangular. Taking the six Costa Rican species of which I have females, the apices of the lobes reach to from .4 to .65 of the length of the lateral margin of abdominal segment nine, and the lamina is bifid in the distal .4 to .62 of its length. Details are given *pos ea* under each species, but I believe that the range of variation in these dimensions is partly, perhaps largely, due to differences in the drying of specimens.

Dr. Ris, after describing the structure of the posterior abdominal segments of the female of *E. obtusus* from Peru as typical of the genus, adds: "Die sehr eigenartige Bildung erweckt die Vermutung, dass die Eier in engen Spalten abgelegt werden (vielleicht Zwischen die Blätterbasen der Bromeliaceen, wie bei *Mecistogaster*?)." ¹⁹ On looking through my field notes made in Costa Rica the only reference to oviposition of *Epigomphus* which I find is in connection with *E. subsimilis* at Turrúcares, on August 14, 1909, and is as follows: "*Epigomphus* oviposits unaccompanied by ♂; its eyes deep blue above in life." In the absence of mention of any peculiar ovipositing habit, I infer that *Epigomphus* then and there dropped her eggs in water as most North American Gomphines do. I can not recall any details of the observation to which this note refers.

From two females of *E. subsimilis* at Turrúcares eggs were obtained and from them larvae were reared through at least

¹⁸See fig. 3, pl. viii, Ent. News, xiv.

¹⁹Archiv f. Naturges., 82 Jahrg., Abteil A, 9 Heft, p. 153.

two instars. These larvae are reserved for treatment in another paper to deal with immature stages of various Odonata.

SYNOPSIS OF THE SPECIES AND NOTES ON THEIR COLORS, VULVAR LAMINAE, ETC.

In my paper of 1903 and again in the *Biologia* volume (1905), I gave synopses of species of *Epigomphus* arranged in the form of keys for identification. The primary division of both these synopses was based on the second pale antehumeral stripe, since this is a character common to both sexes. Males and females were then treated separately under each of these two primary divisions, fewer species being known in the female sex than by males.

Dr. Ris has also given a "Tabelle der ♂" grouped primarily on the form of the inferior appendage, the second pale antehumeral stripe being assigned a secondary position.

In view of the existence of these three keys it seems unnecessary to give one here for the males, although the males of *verticicornis* and, of course, of the new species here described (*subsimilis*) are not included in any one of them. The description of the male of *verticicornis*²⁰ is so drawn up that the differences from other species can readily be seen by comparison with the synopsis in the same work, and the description of *subsimilis* herewith presented follows the same plan. It appears worth while to attempt a key for the females of this genus, since I know them in a greater number of species than in 1905, and since a character of which I then made some use (the spines of the third femora) appears to be too variable to serve as a specific differential.²¹

It should be pointed out here that what I call the "occiput" corresponds to what Dr. Ris calls the "occipital platte," and that what he names the "hintern Flache des Occiput" is the rear of the head in my nomenclature, as I incline to the view that this area is post-genal rather than occipital.

²⁰Biol. Cent.-Amer., Neur., p. 410, 1908.

²¹Cf. the description of the female of *verticicornis*, *loc. cit.*

Key to the Females of Costa Rican Epigomphus

- I. One pale green or yellow antehumeral stripe and a more posterior pale green or yellow antehumeral spot, the latter representing the upper end of the second antehumeral stripe of §II.

Behind each lateral ocellus no tubercle projecting markedly above the level of the ocellus itself.

Vertex without five longitudinal grooves, occiput without a strong postero-superior tubercle at each lateral extremity.

In dorsal view each lateral ocellus subequally distant from the mid-dorsal line of the head and from the adjacent eye-margin.

subsimilis, new species

In dorsal view each lateral ocellus two to four times as far from the mid-dorsal line of the head as from the adjacent eye-margin.

quadracies

Vertex with five longitudinal grooves, one median, two lateral ocellar and two parocular; occiput with a strong posterior or postero-superior tubercle, or rounded horn, at each lateral extremity.

tumefactus

Behind each lateral ocellus a stout tubercle projecting much above the level of the ocellus itself. (Differs from *armatus* also in having no such deep pits on the rear of the head. Cf. figs. 25, 26, 29, 30, pl. XV)

verticicornis

- II. Two narrow pale green or yellow antehumeral stripes, the posterior one close to the humeral suture.

Behind each lateral ocellus no tubercle projecting dorsad markedly above the level of the ocellus itself. **subobtusus**

Behind each lateral ocellus a stout tubercle which projects dorsad markedly above the level of the ocellus itself. Rear of the head with a much deeper pit each side than in the preceding species.

armatus

The female of *E. camelus* is still unknown.

The structure of the head of the females is described under the section of this paper entitled "Mutual Mating Adaptations," pages 338-352. It is, therefore, omitted from the following notes on some of the species.

Epigomphus camelus

Epigomphus camelus Calvert, Biol. Cent-Amer., Neur., pp. 170, 172, tab. viii. figs. 1-3 (apps. ♂), 1905.

The following is based on the three males listed *antea*, page 325.

♂. Pale color (blue?) on the dorsal surface of the frons separated into two spots, right and left, by a narrow median blackish stripe.

Metepimeron with a dark brown stripe along its ventral margin, parallel to the brown stripe on the second lateral suture and at mid-length wider than the pale yellow which separates it therefrom.

Abdominal segment two with a narrow, mid-dorsal, longitudinal, yellow stripe reaching caudad to the transverse anteapical row of denticles and bordered on each side with brown; three with a mid-dorsal, longitudinal, yellow line which is not confluent with yellow on each side of the segment, which lateral yellow extends for almost the entire length thereof; four to six with a mid-dorsal, basal, yellow spot, occupying the basal fourth on four, less on six, not confluent with yellow on the sides in the basal third of each segment; seven yellowish in its anterior half or slightly more, except for a transverse brown stripe at one-third of the segment's length, remainder blackish brown; eight to ten blackish brown with indefinite yellowish or reddish-yellow markings on the sides.

Vertex similar to that of *subsimilis* ♂, occiput with two prominent transversely elongated convexities which occupy almost its entire dorsal surface, no dorsal pits or posterior tubercles; rear of the head undifferentiated.

Abdomen 37 to 40 mm.; hind wing 34 to 36 mm.

***Epigomphus subsimilis* new species** (Pl. XIII, figs. 1 to 7.)

♂. Abdominal segment eight distinctly wider at its posterior end (2.5 to 2.8 mm.) than at its anterior end (1.1 to 1.6 mm.), nine subequal in width to the hind end of eight, but widening slightly caudad, ten a little wider (2.8–3.2 mm.) than the hind end of nine and distinctly higher (2.7–2.9 mm. *vs.* 1.75–2.1 mm.), its dorsal surface convex when viewed from behind but without a tubercle, having two dorsal groups, one right and one left, of two to eight spinules and on each lateral surface a group of similar more numerous spinules.

Superior appendages 1.25–1.5 mm. long, shorter than nine, each one, in dorsal view, having the inner (mesal) edge slightly concave, the outer (lateral) edge almost straight, the two edges distinctly divergent from base to apex, apex truncate a little obliquely mesad and caudad, the inner (mesal) angle the more acute; in profile, the upper and lower edges convergent, the upper edge longer and slightly convex, the lower slightly concave, the lateral apical angle of the dorsal view not projecting below the lower edge (when the appendages are *not* spread apart, as is usually the case in specimens which have not been prepared in the way that the original of our fig. 2 has been) but the mesal apical angle produced ventrad below this edge as a moderately curved subacute process.

Inferior appendage a little longer than the lower edge of the superiors, hence projecting a short distance beyond the latter, bifid in its distal half, the apices of the two branches less distant than the apices of the superiors; in profile the tip of each branch is shallowly bifid the upper division stouter, more rounded, recurved, the lower a little longer and directed caudad and slightly dorsad. Dorsal surface of the appendage concave, mesal margins of its two branches elevated and with a conical tooth at the proximal sixth; right and left margins of the whole appendage diverging slightly, the distance between the tips of its branches (1.4 to 1.5 mm.) greater than the width (.7 mm.) of either branch at base, opposite (*i. e.*, mesal) edges of the two branches diverging strongly throughout.

Each lateral ocellus on the summit of an elevation a little nearer to the mesal margin of the adjoining eye (.21 to .28 mm.) than to the mid-dorsal line of the head (.35 to .42 mm.). Meso-caudad of each ocellus and on the elevation is a ridge or wall, subparallel to the ocellar margin, which rises almost, but not quite, as high as the ocellus itself, its crest rounded, the ridges of the right and left sides connected on the mid-dorsal line so that in dorsal view they present the appearance of an inverted W, the angles of which are rounded in some specimens; there is some tendency to prolong this ridge on the lateral side of the elevation, as in *subobtusus*, but it is not as strongly manifested as in that species where the ocellar elevations are lower. Elevations of the right and left ocelli separated by a depression which, in posterior view, is about as deep as one-half of the height of either elevation.

♀. Vertex similar to that of the ♂, the distance of the lateral ocelli from the mid-dorsal line of the head a little greater (.49 mm.) in some, the depression between the two elevations deeper in some.

Vulvar lamina .77 to .84 mm.²² long, reaching to half of the length of the lateral margin of segment nine, bilobed in the apical .46 (average of 7 ♀, range .42-.58, cf. page 330, *antea*) of its length, interval between the lobes triangular.

♂ and ♀. Pale color on the dorsal surface of the frons separated into right and left spots.

Metepimeron with a dark brown band on or near its ventral margin, parallel to, but separated from, the brown band, of the second lateral suture by pale green or yellow of more than its own width; absent in the two alcoholic females (otherwise well preserved as to color) and indistinct in some of the dry specimens of the same sex.

Abdominal segment two with a mid-dorsal, longitudinal, yellow stripe for more than half the segment's length, reaching or not reaching the extremities of the segment, bordered on each side by brown; three to six chiefly ochraceous, blackish brown in the apical fourth, less defined in the ♀; seven paler, green or yellow, in the anterior three-fifths, blackish brown in the remainder; eight to ten blackish brown, sides yellowish inferiorly in the ♂, indistinctly so on eight in the ♀.

Abdomen, ♂, 38 to 41, ♀ 42 to 46; hind wing, ♂, 34 to 35, ♀, 37 to 40 mm.

Type.—♂; Turrúcares, Costa Rica, August 14, 1909, taken by P. P. Calvert. *Allotype*.—♀; same locality, date and collector. *Paratopotypes*.—3 ♂, 6 ♀; all as listed *antea*, page 325.

The specific name proposed alludes to the greater degree of resemblance in the vertex and occiput of the two sexes than prevails in the other Costa Rican species here treated.

²²The measurements here and elsewhere in this paper for the vulvar laminae are made by eye-piece micrometer with a Zeiss binocular microscope, paired oculars 4, objectives F 55.

Epigomphus quadracies

Epigomphus quadracies Calvert, Ent. News, xiv, pp. 188, 189, 190, 191. 1903. Biol. Cent.-Amer., Neur., pp. 170, 171, 172, tab. vii, fig. 36 (occiput ♀), tab. viii, figs. 4, 5 (apps. ♂). 1905. Ris, Archiv. f. Naturgesch., 82 Jahrg., Abteil A, 9 Heft, p. 150. 1918.

The following notes are based on the material listed *antea*, page 325:

Pale color on the dorsal surface of the frons separated into two spots, right and left, in all except the male of August 4. No dark band on or near the ventral margin of the metepimeron.

Abdominal segment two with a mid-dorsal, longitudinal, yellow stripe which reaches the hind end and is bordered on each side by blackish brown (♂), more indistinct and bordered by brown or ochraceous in the ♀; three to six blackish brown with a mid-dorsal yellow or ochraceous line, or this line on three and four only, five and six with a small, mid-dorsal, basal yellow spot (Panama ♂); three with a longitudinal, lateral, yellow stripe on its anterior five-sixths, four to six with a basal, lateral, yellow spot; seven with anterior half to three-fifths (♂) or third (♀) ochraceous, pale green or yellow, remainder blackish brown or brown; eight to ten blackish brown, the males with a variable extent of yellowish inferiorly on the sides.

♀. Vulvar lamina .63-.7 mm. long, reaching to .4-.5 of the lateral margin of segment 9, bilobed in its distal .4-.5, interval between the lobes triangular.

Abdomen, ♂, 35 (Alajuela), 39 to 39.5 (Rio Chirripo); ♀, 40 to 42 (both localities); hind wing, ♂, 30 (Alajuela), 32 (Rio Chirripo); ♀, 34.5 to 35 mm. (both localities).

Epigomphus tumefactus

Epigomphus tumefactus Calvert, Ent. News, xiv, pp. 188, 190, 191, pl. viii, fig. 4 (entire ♂). 1903. Biol. Cent.-Amer., Neur., pp. 171, 172, tab. viii, figs. 6, 7 (apps. ♂). 1905. Ris, Archiv. f. Naturgesch., 82 Jahrg., Abteil A, 9. Heft., pp. 146, 147, 149, figs. 94, 95 (apps. ♂). 1918.

The following notes are based on the material listed *antea*, page 325:

Pale color on the dorsal surface of the frons narrowly (♂) or widely (♀) separated into two spots, right and left.

Metepimeron with a brown band on or near its ventral margin in the males from Peralta and Guapiles, faint in the Estrella ♂ and Guacimo ♀, absent in the other three females.

Abdominal segment two with a yellowish, longitudinal, mid-dorsal stripe bordered on each side by brown; three to six blackish, three (or three and four, ♀) with a mid-dorsal, longitudinal, yellow line, four to six with a mid-dorsal, basal, yellow spot; three with yellow on the sides for the anterior three-fourths, not confluent with the dorsal yellow; four with yellow on the sides for the basal third to almost the entire length, usually not confluent with the dorsal yellow; five to six yellow on the sides for the basal sixth to two-thirds, usually not confluent with the dorsal yellow; seven with the basal four-to five-sevenths (♂), two-to three-sevenths (♀) yellow, except for a transverse brown line each side at two-sevenths of the segment's length,

the remainder of the segment brown; eight to ten blackish brown with a variable extent of yellow on the sides inferiorly.

♀. Vulvar lamina .91 to .98 mm. long, reaching to .44 to .54 of the length of the lateral margin of segment nine, bilobed in the distal .54 to .58 of its length, interval between the lobes triangular.

Abdomen, ♂, 40 to 42, ♀, 44 to 47; hind wing, ♂, 34.5 to 36, ♀, 38 to 39 mm.

Epigomphus verticicornis

Epigomphus verticicornis Calvert, Biol. Cent.-Amer., Neur., p. 410. 1908.

The following notes are based on the type ♂ and allotype ♀ listed *antea*, page 326:

Pale color on the dorsal surface of the frons narrowly (♂) or widely (♀) separated into two spots, right and left.

Metepimeron with a brown stripe near the ventral margin, but not reaching the entire length of the sclerite, parallel to, but separated from, the brown stripe on the second lateral suture by pale green of more than its own width.

Abdominal segment two faded in the ♂, with a narrow, mid-dorsal, yellow stripe reaching to the transverse anteapical denticles and bordered with brown on each side (♀); three to four with a mid-dorsal, longitudinal, yellow line and yellowish laterally for much of their length, confluent in the ♀ with the dorsal yellow at the base of three but not on four; five and six faded in the ♂, in the ♀ with a small, basal, mid-dorsal, yellow spot and the sides yellow in the basal third, not confluent with the dorsal yellow: seven faded, yellowish on the anterior five-sixths (♂) or half (or more? ♀), blackish in the remainder; eight to ten blackish with ill-defined yellowish or reddish-yellow on the sides (♂, but not ♀).

Epigomphus subobtusus

Epigomphus subobtusus Selys, Bull. Acad. Roy. Belg. (2), XLVI, p. 467, 1878. Quatrièmes Addit. Syn. Gomph., p. 62, 1878. Calvert, Ent. News, xiv, pp. 189, 190, 191, pl. viii, figs. 10, 11 (3rd tibia ♂), 1903; Biol. Cent.-Amer., Neur., pp. 171, 172, 399, tab. vii, fig. 37 (occiput ♀), tab. viii, figs. 8, 9 (apps. ♂), 1905, 1907; A Year of Costa Rican Nat. Hist., pp. 149, 207, 1917. Ris, Archiv f. Naturgesch., 82 Jahrg., Abteil A, 9 Heft, pp. 146, 147, 150, 1918. Calvert, Ent. News, xxx, p. 36, 1919.

In the book of 1917 above cited we have referred to the case of mimicry observed at Quebrada Honda, Costa Rica, between this species and *Brechmorhoga rapax crocosema*. Following is a fuller statement of the observation from my field note book.

On August 1, 1909, at a small stream, descending from woods high above the railroad tracks by a series of cascades through steep fields of garlic (or onions), beets, manihot, etc., and passing under the tracks west of the bridge over the Quebrada Honda

the following Odonata were observed: *Brechmorhoga rapax crocosema* Ris, *Epigomphus subobtus* Selys, *Paltothermis lineatipes* Karsch, *Hetaerina cruentata* Ramb., *Argia extranea* Hagen and *Cora chirripa* Calvert. A marked similarity in color and manner of flight between the *Brechmorhoga* and the *Epigomphus* was noted. They were found at the same spot in the stream. The resemblances observed were:

The approximately equal length of body, the abdomen widest at or near its hind end, the blue (*Epigomphus*) or bluish-green (*Brechmorhoga*) eyes, the thoracic pattern—dark brown with pale oblique bluish or greenish stripes, the abdomen dark brown with bluish (*Epigomphus*) or greenish (*Brechmorhoga*) longitudinal markings at the bases of segments three to five or six, the seventh segment with a more conspicuous pale marking than on any other part of the body.

The differences other than those of taxonomic value are:

The more robust form and wider wings of *Brechmorhoga*, the widening of the abdomen on segments eight to ten in *Epigomphus*, on six to seven in *Brechmorhoga*; the metallic green of the frons of *Brechmorhoga*, pale blue in *Epigomphus*, the wider pale stripes on the thorax of *Brechmorhoga*, the pale mark of abdominal segment seven in *Brechmorhoga* deep yellow, in *Epigomphus* pale blue.

While the manner of flight is similar, *Brechmorhoga* stays longer on the wing and poises longer in the air, while *Epigomphus* tends to alight more frequently. *E. subobtus* and other species of its genus curl the hind end of the abdomen ventrad very often when flying about.

When referring to these observations in 1917 we pointed out that: "There was nothing in this case, however, to suggest that the resemblance offered a means of defense to either species against enemies."

The following notes are based on the material listed *antea*, page 326, and on two males three females from Cayuga, Guatemala, April 25, May 3, 8 and 28 taken by Messrs. Schaus and Barnes, included in the paper of 1919.

Pale color of the dorsal surface of the frons not separated into two spots right and left in all five males and the Juan Viñas female; so separated in three females, that of April 25 being uncertain.

Metepimeron with a brown stripe as described for *E. subsimilis*, not reaching the whole length of the sclerite.

Abdominal segment two with a longitudinal, mid-dorsal, yellowish²³ stripe

²³Color as seen in the dried specimens. Compare the statements given above for the living colors.

bordered on each side with brown; three to six dark brown, with a mid-dorsal, longitudinal, pale line, or on three and four only, five and six with a small basal spot; three with a yellowish stripe each side from base almost to apex; four to six with a yellowish spot or stripe each side occupying the anterior fourth to seven-ninths on four, fourth to five-sixths (but then less distinct) on five, fourth to third on six; seven yellowish in its anterior three-fifths to four-fifths, except for a transverse brown line each side at one-third of the segment's length, the remainder brown; eight to ten dark brown with indistinct yellowish markings on each side inferiorly for the entire length of these segments.

♀. Vulvar lamina .84 to .91 mm. long, reaching to .4 to .65 of the length of the lateral margin of segment nine, bilobed in the distal .5 to .62 of its own length, interval between the lobes triangular.

Epigomphus armatus

Epigomphus armatus Ris, Archiv f. Naturgesch., 82 Jahrg., Abteil A. 9, Heft, pp. 146, 147, 148, figs. 90 (thor. pattern), 91-93 (apps. ♂), 1918.

The following notes are based on the material listed *antea*, page 326:

♀. Pale color on the dorsal surface of the frons widely separated as two spots, right and left.

Metepimeron apparently with no dark stripe near its ventral margin (none shown in Dr. Ris' figure 90).

Abdominal segment two faded, apparently with a broad, basal, dorsal, yellowish area contracted on the posterior half of the segment to a narrow, longitudinal stripe, stripe bordered each side with brown; three to six with a mid-dorsal, longitudinal, yellow line apparently confluent at base with yellow which extends the entire length of the sides but is crossed by a transverse blackish line at one-third the length of each segment; seven yellowish, only a similar transverse stripe and the hindmost sixth of the segment blackish eight to ten blackish, yellowish on the sides inferiorly for most of the length of eight and indistinctly on nine.

♀. Vulvar lamina .77 to .84 mm. long, reaching to .57 to .59 of the length of the lateral margin of segment nine, bilobed in the distal .45 to .5 of its length, lobes more nearly parallel than in the other species, but this may be due to individual or mechanical conditions of the specimens.

MUTUAL MATING ADAPTATIONS

Soon after making my collection of Odonata in Costa Rica I noticed the modifications which the specimens of *Epigomphus* presented and made this note for my future guidance: "A comparative study of the shapes of the apps. ♂ and the vertex, occiput and rear of head ♀ ought to give some interesting sexual co-adaptations." In 1910, Dr. F. Ris interpreted ²⁴ the presence of certain scars on the compound eyes of females of *Anax*

²⁴Kopulationsmarken bei Libellen. Deutsche Entom. National-Bibliothek, 1, pp. 70-80.

parthenope as due to the teeth on the inferior appendage of the male, applied against the dorsal surface of her head when pairing. These scars (which I also have found in females of *A. junius*, *A. parthenope* and *A. imperator*) are, he noted, accompanied in some cases with a coagulated crust which, he suggested, might be derived from a secretion of the male, or exuded blood or lymph of the female. Dr. E. M. Walker has described and figured²⁵ the copulatory position of the male appendages of *Gomphus spicatus*, in which they are represented as being stretched apart rather widely, and I have made some suggestions as to the probabilities in *Erpetogomphus tristani*.²⁶ Dr. C. H. Kennedy has figured and briefly described²⁷ the manner in which the appendages of the male of the Californian *Octogomphus specularis* clasp the head of the female. In describing *Epigomphus armatus*, Dr. Ris remarks: "Die Struktur des ♀ Occiput ist ein sehr schönes Beispiel von Anpassung des ♀ an die Klammerfunktion des ♂ Appendices,"²⁸ although he does not point out the adaptations in detail.

Availing myself of these observations and suggestions, I have attempted, in the following pages, to correlate definitely the structures of the two sexes when in the copulatory position. I hope that other students may be able to correct or improve upon what is here offered. *Epigomphus verticicornis* is considered first because the evidence seems fullest for that species.

Epigomphus verticicornis (Pl. XV, figs. 23 to 26.)

Of *Epigomphus verticicornis* I have only two specimens, the type male and allotype female from Tuis, taken by Mr. C. H. Lankester, which, as stated in the *Biologia* volume, p. 410, "communicated by Prof. Biolley, were taken in June, 1907, and sent enclosed in the same envelope, whence it is concluded they were pairing."

This female has on the rear of the head behind the right eye, at about the same horizontal level as the mesal angulation of

²⁵The North American Dragonflies of the genus *Aeshna*. University of Toronto Studies, Biological Series No. 11. pp. 41-42, pl. 2, fig 7, 1912.

²⁶Ent. News, XXIII, pp. 294-295, 1912.

²⁷Proc. U. S. Nat. Mus., 52, p. 578, figs. 332, 333, and p. 579, 1917.

²⁸Archiv f. Naturgesch., 82 Jahrg., Abteil. A, 9 Heft, p. 149, 1918.

the posterior eye margin, a group of three contiguous scars or depressions (Pl. XV, fig. 26, *pgc*) and in the corresponding position behind the left eye two groups of two scars each. The distance beyond the right and left groups is very nearly equal to the distance between the apices of the right and left superior appendages of the male, when these are spread apart as in Pl. XV, fig. 24, *pgc'*. It seems highly probable, therefore, that when pairing the apices of the superior appendages of the male were applied against the hind surface of the female's head at the positions now indicated by the scars, the scars being produced by the tooth at the apex of each appendage. The fact that there is more than one scar on each side of the female's head may be readily accounted for by supposing that a permanent hold was not immediately secured, and that some slight shifting of the male's appendages occurred in the attempt, or that two or more males may have paired with this female, as Dr. R. T. Hance suggests.

These *post-genal* scars, or *cicatrices*, as they may be termed, lie in a wide and shallow groove which extends from its upper end obliquely ventrad and mesad. This groove is bounded superiorly by a transverse ridge whose summit is rounded off; above this ridge are nine or ten subvertical impressed lines (Pl. XV, figs. 25, 26, *ll*) such as are found in corresponding positions on the female of *E. tumefactus* (Pl. XIV, fig. 22, *ll*). Two possibilities are suggested by the existence of these impressed lines: (1) that they may serve as guides to direct the apices of the male's superior appendages when he is attempting to grasp the female's head, and hence must exist before pairing, or (2) that they are produced by the tooth on the tip of those appendages when he makes that attempt and that in consequence they also are cicatricial. Against this latter view is the circumstance that the area over which they are found is much wider than the area covered by the above-described post-genal cicatrices, whereas one would expect approximately as many cicatrices as impressed lines. It should be noted that the distribution of these impressed lines is not exactly symmetrical on the two sides of the head.

A slight linear depression (Pl. XV, fig. 26, *x*) mesad to the lower end of the most mesal of these impressed lines may possibly

receive (or be caused by ?) the "downwardly-directed spine"²⁹ of the inner surface of the left superior appendage of the male (Pl. XV, fig. 23, *x'*); this slight depression is present also, but less marked, on the right side of the head, although this spine is absent on the right superior appendage of the single male; perhaps its presence on the right side of the female's head is confirmatory of Dr. Hance's suggestion and this female may have paired also with a male which had this spine present on both superior appendages.

On the dorsal surface of the head of this female certain scars are visible. The best marked are a group of two (right) or three (left) near the mesal margin of the faceted portion of the compound eyes, at the same transverse level as the horns behind the lateral ocelli ("vertex tubercles"). Between each group and the nearer lateral ocellus another scar is visible in a groove on the vertex, the *parocular sulcus* (*prs*), close to and paralleling the eye margin. Parocular scar and eye scars together constitute a group of *superior ocular cicatrices* (Pl. XV, fig. 25, *soc*). The distance from the right group of these *cicatrices* to the left group corresponds very closely to the distance between the apices of the two branches of the inferior appendage of the male (Pl. XV, fig. 24, *soc'*) and the *cicatrices* are doubtless produced by the two teeth on each side of these apices. There is what seems to be a scar posterior to each "vertex tubercle," between it and the occipital tubercle of the same side of the head, but I am unable to correlate these scars with any projection on the dorsal surface of the male's inferior appendage, as the "fairly slender forwardly-curved spine" thereof (Pl. XV, figs. 23, 24 *y*) is situated at a greater distance from the apices of the inferior appendage than exists between these scars and the superior ocular *cicatrices* of the same side of the head. It seems more likely that these spines of the male come in contact with the occiput, but I find nothing there of such a shape as would engage these spines. The wide, concave, distal margin of the inferior appendage of the male is doubtless applied against the posterior surfaces of her two postocellar or vertex tubercles (*poct*), while her occipital tubercles (*dot*) are

²⁹The words enclosed in quotation marks are from the original description in Biol. Cent.-Amer., Neur., p. 410.

probably received into two shallow depressions (*dot'*) of his appendage which lie immediately distad and slightly mesad of his forwardly-curved spines, the latter, therefore, apparently lying just laterad of the occipital tubercles when pairing, perhaps in the parocular grooves.

The extent to which the head of the female of this species has been modified in apparent correlation with mating may be seen from the following details of the structure of the head of the male.

The vertex of the male and that of the female are dissimilar, the former being like that of *quadracies* male (except that the lateral ocelli are not so near to the eye margins) and of both sexes of *subsimilis*, and lacks the conspicuous postocellar, or "vertex, tubercles" of the female.

The occiput of the two sexes is dissimilar in that the male has shallow pits dorsally where the female has tubercles and the posterior surface smoother and less swollen.

The rear of the head (postgenae) of the male has no transverse rounded ridge and but very few traces of the subvertical impressed lines of the female.

Epigomphus armatus (Pl. XV, figs. 27-30.)

Of this species, recently described by Dr. Ris, I have two females but no males. He has figured the appendages of the male and I copy two of his figures; in the specimen from which figure 27 was made the superior appendages were apparently not as widely distended as they are in the act of pairing. The apices (*p'*) of the male's superior appendages are, doubtless, received into the very deep pits (Pl. XV, fig. 30, *p*) of the rear of her head. One of my females has distinct superior ocular cicatrices near the angle of the mesal margin of the eyes. By analogy with *E. verticicornis*, I would expect that the apical (distal) margin of the male's inferior appendage would, when pairing, be applied against the posterior surfaces of the two postocellar, or vertex, tubercles ("kräftige hornartige Fortsätze" of Dr. Ris) of the female. A comparison of fig. 27 with fig. 29 shows, however, that if the apices (*soc'*) of his inferior appendage cause the cicatrices, *soc*, the shape of the distal margin of the appendage is such that it would then lie some distance away from and caudad to the post-ocellar tubercles.

In the absence of male specimens I am unable to make any further suggestions.

Dr. Ris has described the vertex of *armatus* male which lacks the postocellar tubercles.³⁰

Epigomphus tumefactus (Pl. XIV, figs. 20 to 22.)

On the dorsal surface of the head of the female there is a distinct *parocular groove* (*prs*) along the mesal margin of each eye from the antenna almost to the occiput; it is deepest at its posterior end. Between the right and left parocular grooves are three other longitudinal grooves each delimited laterad by distinct longitudinal ridges. The median of these may be called the *median vertex groove* or *sulcus* (*mvs*) and extends from the frons almost to the occiput; it is wider anteriorly, where it lodges the median ocellus, narrows to its mid-length, thence widens slightly to its posterior end. The other two grooves may be styled *paramedian* or *lateral ocellar sulci* (*los*) and extend almost from the hind margin of the frons almost to the occiput; the ocellus in each groove is situated on the mesal slope thereof. All five grooves are barred from reaching the occiput by a low transverse, posterior, terminal ridge of the vertex (Pl. XIV, fig. 21, *tr*) reaching from eye to eye.

The female from the Florida Road, of June 3, has a marked superior ocular cicatrix on the right eye at its mesal margin opposite to the ocellus of the same side, a scar which extends into the right parocular groove. In the corresponding part of the left parocular groove there are three or four slight impressions, close together, which may be cicatrices, but there is nothing of the kind on the left eye.

The occiput has a pair of low transversely elongated tubercles or low ridges (fig. 21, *dor*) in the middle two-fourths of its dorsal surface, its hind margin is distinctly and narrowly emarginated in the middle and there is a strong tubercle with blunt, rounded apex (*pot*) on the posterior surface laterad to the level of the mesal angle of the dorso-mesal margin of each compound eye.

On each side of the rear of the head, at about one-third of the distance from the lateral end of the occiput to the outer surface of the eye is a subvertical ridge (fig. 22, *r*), on the mesal side of which is a pit (*p*, same figure) and on the lateral side a distinct subvertical groove (*g*). From the pit and a wide shallow trough running from it mesad and ventrad extend mesad and dorsad

³⁰Archiv f. Naturgesch., 82 Jahrg., Abteil. A, 9 Heft, p. 147.

about eleven impressed lines (*ll*), some of them subparallel to their next neighbors, others diverging; the more dorsal of these are nearer together.

No post genal cicatrices are visible on this female. That of June 6 shows what may be faint scars but these are asymmetrically placed. The female taken by Biolley presents two pairs of approximately bilaterally symmetrical scars, and these have been added to figure 22, *pgc*. The female from Estrella shows no cicatrices, the pit, ridge and groove on each side of the rear of the head are much less pronounced than in the other three females.

The following suggestions as to the relations of the male appendages to the female head, when pairing, seem plausible: That the lateral apical angles (Pl. XIV, fig. 20, *p'*) of his superior appendages are received by the pits *p* (fig. 22), the mesal apical angle and the denticles of the inferior apical margin (*ll'*) fit into some of the impressed lines *ll*; distended still more widely the mesal apical angles may produce the postgenal scars (*pgc*); each strong posterior tubercle, *pot*, of her occiput is received within the concave mesal surface (*pot'*) near the base of his superior appendage of the same side of his body; the apices (*prs'*) of his inferior appendage are placed in her parocular grooves (*prs*), while the transverse dorsal ridges (*dor*) of her occiput are lodged in the concavity (*dor'*) of the dorsal surface of the undivided basal portion of his same appendages; perhaps the dorsal denticles near the apical margin of this latter (Pl. XIV, fig. 20, *d*) may secure some hold on the longitudinal ridges which separate the five vertex grooves of her head.

In the vertex of the male the parocular sulci are present but narrower, the median sulcus is shallower and less sharply defined, the lateral ocellar sulci are much shorter antero-posteriorly as the vertex rises cephalad from its hind margin to an elevation immediately caudad to, and of about the height of, each ocellus, the two elevations thus formed being separated from each other by the median sulcus; the lateral ocellar sulci likewise are much less sharply defined from adjoining sulci than in the female.

The occiput of the male lacks the pair of low transverse dorsal ridges, its hind margin is less emarginated in the middle and the lateral posterior tubercles are much shorter and less pronounced.

On the rear of the male's head, the homologue of the subvertical ridge of the female can be recognized in a similar but more rounded swelling, but pit, groove and impressed lines, as described for her, are absent.

Epigomphus quadracies (Pl. XIII, figs. 8 to 10.)

Of the five females of this species, two show superior ocular cicatrices near the mesal angle of the mesal margin of each eye. One of these (July 25) has each cicatrix (fig. 9, *soc*) consisting of two adjacent impressions in the faceted portion of the eye, accompanied by only a very slight exudation, but otherwise shows no difference in color from adjoining areas of the eye; there is a slight depression on the hind surface of the elevation on which each lateral ocellus is situated; the dorsal surface of the occiput has a pit, (*dof*) occupying each of its lateral thirds, the external (lateral) wall of which is creased and grooved transversely; there is a small, conical, supero-posterior tubercle (*pot*) at each lateral extremity of the occiput; on the rear of the head, behind each eye, at the level of not quite half-way from the mesal angle of the superior surface of the eye to its extreme lateral margin, is a fairly deep pit (fig. 10, *p*), elongated slightly obliquely from above mesad and ventrad; this pit is not as deep as in the female of *armatus*, but is deeper than in any other of the Costa Rican species here considered; as in *armatus*, this pit is bounded mesad by a prominent subvertical ridge (*r*), which in dorsal view appears as a conspicuous rounded tubercle, but the lateral slope of this ridge is more gradual and less steep than in *armatus*; this pit and ridge are above the level of the mesal angle of the posterior margin of the eye; below that level and almost directly ventral to the lower end of the pit is a distinct cicatrix (*pgc*), each consisting of three adjacent impressions (or possibly four on the left), the whole distinctly darker in color than the adjoining areas.

In the female of July 26, the superior ocular cicatrices consist of apparently a single impression each, the cicatrix on the right side of the rear of the head of two adjacent impressions, the corresponding cicatrix of the left side of but one impression; in all other respects this female agrees with the preceding description.

Of the other three females which have no superior ocular cicatrices, two (those of August 8) have the post-genal cicatrices, in one female consisting each of a single impression, but the scar of the right side larger than that of the left, the other female having the right cicatrix of two, the left of one, impression. The third female (August 4) shows no post-genal cicatrices although eggs are adhering to the ninth abdominal sternite and to other parts of her body. In other respects these three females agree with the description given above of the female of July 25.

A comparison of the male appendages and head of the female make it likely that, in pairing, the lateral apical angle (p') of his superior appendages is received into the deep, post-genal pit (p), the mesal apical angle (pgc') of the same causes the post-cephalic cicatrix (pgc), the outer division (fig. 8, soc') of the apex of each branch of his inferior appendage sometimes producing the superior ocular cicatrix (soc) the acute superior basal tooth of each branch of the same appendage entering the superior pit (dof) of her occiput. I had thought at first that the *inner* division of the apex of each branch of his inferior appendage might be applied against the posterior surface of the elevation of her lateral ocellus, but the distance between the superior ocular cicatrix and the slight depression on the hind surface of this elevation of the same side of the head, in the two females which show these cicatrices, is too great to allow one to suppose that these two positions could be occupied by the divisions of the apex at the same time. Whether the cicatrices are made in the attempt to adjust the inner division of the apex to the ocellar elevations, or whether pairing may occur without this adjustment being made, must be determined by actual observations of the insects when mating. It should, however, be pointed out that the superior occipital pits of the female can not receive the superior basal teeth of the branches of the male's inferior appendage when the inner divisions of the apices of those branches are applied against her ocellar elevations, as the distance again is too great.

In the vertex of the male each lateral ocellus lies on the summit of an elevation which summit is much nearer (.14 mm.) to the mesal margin of the adjoining compound eye than to the mid-dorsal line of the head (.56 mm.); meso-caudad to each ocellus, but lower on the elevation, is a ridge or "wall" (Ris) whose crest is rounded and which in dorsal view shows as a curve with its convexity cephalad, the curves behind the two ocelli meeting on the mid-dorsal line; this ridge at no point is as high as the ocellus, as is the case in *E. subobtus*. The elevations of the right and left ocelli are separated by a depression, which in posterior view is not deep as one-half of the height of either elevation.

In the vertex of the female the ridge or wall is lacking or indistinct and the depression between the two ocellar elevations is deeper, being more than one-half as deep as the height of either elevation when viewed from behind. The lateral ocelli are situated with respect to the compound eyes and the mid-dorsal line as in the male.

The occiput of the male has shallower dorsal pits and no supero-posterior tubercles, and the rear of his head is not differentiated into pit and ridge behind each eye.

Epigomphus subsimilis (Pl. XIII, figs. 1 to 3, 5 to 7.)

Of the seven females of this species none show any scars on the eyes or in the region of the ocelli comparable to those observed and described for *E. verticicornis* and other species, although two of these females yielded eggs from which larvae subsequently hatched, so that these two females must have paired. On the rear of the head, laterad to the level of each lateral end of the occiput (and consequently laterad to the level of the meso-dorsal margin of each compound eye) is a moderately deep pit (fig. 7, *p*); in each of these is one or two impressions which are probably cicatrices. Laterad to each pit is the inferior end of a pronounced vertical ridge (*r*, same figure), the end of which appears as a tubercle in a dorsal view of the head (fig. 5, *r*). Laterad this ridge is sharply delimited by a subvertical groove (*g*). A comparison of the male abdominal appendages and the female head makes it likely that when pairing the mesal apical angle of his superior appendage, with its ventral subacute process (fig. 2, *p'*) is received into the pit (*p*) and that the lateral apical angle (*g'*) of the same enters the groove, *g*, perhaps near or at its superior end. The position assumed by his inferior appendage is much more conjectural, but a reasonable hypothesis would be that the two apices thereof (*prs'*) are lodged in her parocular grooves (*prs*) between the lateral ocelli and the mesal margins of the eyes.

There are no such pronounced tubercles posterior to and distinct from the elevations on which the lateral ocelli lie as in *E. verticicornis*. The slope cephalad from the occiput to these ocelli is gradual, whereas in *verticicornis* the posterior wall of each post-ocellar tubercle rises almost vertically, thus furnishing a firm support against which the distal margin of the male's inferior appendage may be braced when pairing. Here no such possibility apparently exists.

On the dorsal surface of her occiput are two pits (fig. 5, *dof*) near the two lateral ends thereof; their appearance suggests that of the similarly situated depressions in some females of

E. subobtus referred to *postea* under that species, but in none of the seven females of *subs similis* is there any suggestion of tubercles replacing them.

The vertex and occiput of the male are similar to those of the female but the rear of his head is not differentiated into pit, ridge and groove. The vertices of the two sexes have been compared *antea*, page 334.

Epigomphus subobtus (Pl. XIV, figs. 15 to 17.)

In this species the adaptations of the head of the female to the appendages of the male seem to be less marked than in any of the other species here treated. Two females from Costa Rica and three from Guatemala (as mentioned *antea*, pages 336 and 337) are before me. I find on the right side of the rear of the head of the female from south of Aguacaliente (fig. 17) what I take for a scar with some dried exudations attached; it is very distinct, is elongated, subvertical, its position corresponds to a level of about three-fifths the distance from the mesal eye margin of the dorsal surface of the head to the lateral surface of the eye, and its inferior end is on the same horizontal level as the mesad-directed angle of the posterior eye margin. It appears to correspond to the pit (*p*) rather than to the postgenal cicatrix of other species. No scar is observable on the left side of the head, not even in the "geringe Andeutung einer Struktur von der Art des *armatus*-♀; eine flache Vertiefung, neben der Medialwärts eine Wölbung steht, die aber in der Dorsalansicht nicht sichtbar³¹ ist," described by Dr. Ris. No similar scars are visible on the heads of the other four females, nor do I find any scars on the dorsal surface of the head in any of the five specimens.

By analogy we should expect, of course, that the superior appendages of the male are applied against the rear of the head of the female, when pairing, and that the scar (*p*) above described marks the contact made by the lateral apical angle (*p'*, fig. 15) of the right appendage.

In both the description and figure of the female occiput in the *Biologia* volume I have indicated the presence of a pair of well-marked superior tubercles. Dr. Ris does not mention these and I find the following conditions to exist with respect to them in the present material. In the female from south of Aguacaliente, C. R., both of these tubercles are well developed and similar to the *Biologia* figure (figs. 16, 17, *dot*). In the female from below Juan Viñas

³¹In the five females before me the "Wölbung" is visible in what I should call a dorsal view of the head; cf. fig. 16.

the right tubercle is fairly conspicuous, while the site of the left one is indicated by a pit whose appearance suggests the possibility of its being the tubercle invaginated. The three females from Cayuga, Guatemala, are less mature than those from Costa Rica and may even be described as teneral; one of them (May 8) has the tubercles similar to the condition described for the Juan Viñas female, except that the left tubercle appears to be partly everted from its pit, the other two have a pit in the place of each tubercle, the margins of the pits more or less elevated as minute ridges. There is also a posterior tubercle (*pot*) on the occiput near each lateral end.

The distance between the apices of the inferior appendage of the male is distinctly greater than that between the pits or tubercles of the dorsal occipital surface of the female. It therefore seems unlikely that there is any correlation here, but that those apices rest, when pairing, farther cephalad on her head, probably in the parocular groove (*prs*) between the eye and the lateral ocellus of each side. In that case, a pair of shallow concavities (fig. 15, *dot'*) on the dorsal surface of the undivided basal part of this appendage, situated just proximad to the bases of the two branches, may receive the superior occipital tubercles of the female. Whether the pressure on these tubercles is ever sufficient to flatten them, or whether the eversion of the tubercles is a concomitant of the age or development of the individual female, and so would give the explanation of the differing conditions noted in the specimens above described, are questions which will probably require observations on the living insects to determine. Taxonomically it is important to recognize the differing state of the superior occipital tubercles in what appear to be females of the same species.

The vertex of the male is similar to that of the female.

The occiput of the male has dorsal pits, but less pronounced than in the female, but in no specimen before me has it either dorsal or posterior tubercles. The rear of his head is not differentiated even to the extent of that of the female.

On examining some of the original material of *Epigomphus llama* Calvert from Bolivia, I found a paratypic female from Chulumani, December 3, 1898, showing two well marked post-genal scars at about .35 mm. above (dorsal to) the level of the articulations of the cardines of the maxillae with the head, and about 1.05 mm. below (ventral to) the level of the mesal projection of each posterior eye-margin. I found that I could fit

the appendages of a male from the same locality and date to the head of this female so that the tips of his superior appendages rested in these postgenal scars; with the result that each branch of his inferior appendage came to lie in the parocular groove of the same side of her head, laterad of the ocellus but mesad of the antenna, the tip of each branch reaching cephalad to the superior surface of her frons, the superior anteapical process of each branch being received into the depression behind each of her antennae, the antenna being enclosed caudad by the concavity between the tip of the branch and that process. I was unable to detect any superior ocular scars on her head. Her superior, or dorsal, occipital tubercles are received by shallow concavities at each side of the dorsal surface of the base of his inferior appendage.

The position of the postgenal scars in *E. llama* female is thus much lower than in any of the Costa Rican species studied. This more ventral position is probably due to the more slender form of the superior appendages of the male *llama*, since their absolute length (2.10 mm. in dorsal view) is no greater than that of the same appendages of *E. subobtusus*. The inferior appendage of *llama* male also reaches farther cephalad on the female's head, apparently, than in any of the Costa Rican species. Here again the slenderness of the branches of this appendage is partly responsible for the difference, although the absolute length (2.1 mm. in ventral view) is greater than that of *subobtusus* (1.68 mm.)

It may be that relations similar to those of *E. llama* exist between the male appendages and female head in *E. obtusus* Selys and *E. hylaeus* Ris, also of the South American continent.³² The Brazilian *E. paludosus* has the superior appendages of the male much shorter (1.62 mm.), so that probably they can not reach so far ventrad on the rear of the female's head; his inferior appendage (2.0 mm. long) is not so different from that of *llama* and may take a similar position on her head.

³²See the figures of *E. llama*, Ent. News, xiv, pl. viii, figs. 2 and 7 (1903), and Archiv f. Naturges., 82 Jahrg., Abt. A, 9 Heft, p. 152, figs. 99, 100, (1918), and for *obtusus* and *hylaeus* in the latter, p. 151, figs. 96, 97, and p. 154, figs. 102, 103.

On summing up the data given here and by Dr. Ris it appears that all species of *Epigomphus* thus far studied in both sexes show a differentiation in the two sexes in the rear of the head, this being least marked in *obtusus* and *llama* and most striking in *armatus*. The occiput of the two sexes is similar in *subsimilis* but more or less different in other species, *tumefactus* female showing the most complicated structure of this part. The vertices of male and of female are similar in *subobtusus*, *obtusus* and *subsimilis*, dissimilar in the others, the maximum of specialization being shown by *tumefactus* female in one way and by the females of *verticicornis* and *armatus* in another.

A comparison of the appendages of the males of these species with each other does not furnish any sure basis for deciding that these organs are more specialized in one species than another, since specialization, from a phylogenetic standpoint, may be either by reduction (atrophy) or by complication (hypertrophy). Perhaps we may take the testimony of the other sex on this question and infer that those male appendages are most specialized in the species whose female shows the greatest number of mating adaptations, irrespective of the degree of complication shown by the male appendages themselves.

Judged by similarity in head structure of the two sexes, *subsimilis* is the least specialized of the Costa Rican forms; it is a species in which the second pale antehumeral stripe (of both sexes) is represented only by a superior spot. Of the species which show the greatest differentiation in head structure between the two sexes, *armatus* has the second pale antehumeral stripe complete, while *tumefactus* and *verticicornis* are like *subsimilis* in this stripe.

The data given in this paper would seem to indicate that if the existing species of *Epigomphus* have come into existence gradually, none of them can stand in an ancestral position to any other, but that they represent end twigs of a fairly divergent genetic tree. On the other hand, of course, is the possibility of origin by mutation. By either hypothesis the most interesting feature of their evolution is that the two sexes appear to have been modified correlatively in structures concerned in the act of mating so essential to the continuance of the race. It would be desirable to ascertain whether these correlations are so exact as

to prevent crossing between different "species." A comparison of the figures on Plate XV, illustrating *verticicornis* and *armatus* shows that, although the females of both species agree in possessing strong postocellar tubercles (*poct*), they differ markedly in the rear of the head and in the positions of the superior ocular scars (*soc*), while the appendages of their respective males are very different. The presumption would seem to be that these two species would not cross, but we have as yet no observations to control our speculations. On the other hand, I can see no *a priori* reason why the male say of *quadracies* might not mate with the female of *subsimilis* or of *subobtusius*, but of course mere mechanical ability to pair is no assurance of the production of fertilized ova. It may be that a long time will elapse before we have positive answers to these questions, but their solution should not be of insuperable difficulty.

EXPLANATION OF PLATES

Homologous parts of the heads of females of different species are marked with the same letters. The parts of the males' appendages which receive, or are received by, certain parts of the females' heads are marked with the same letters as the head parts, but with the addition of the prime mark ('). It results that homologous parts of the males' appendages in different species are not always designated by the same letters. The following letters are used in many of these figures:

- dof*, dorsal occipital pit (fossa);³³
- dor*, dorsal occipital transverse ridge;³³
- dot*, dorsal occipital tubercle;³³
- g*, groove on the rear of the head (postgenal sulcus or groove);
- ll*, impressed lines on the same;
- los*, lateral ocellar groove (sulcus);
- mus*, median vertex groove (sulcus);
- p*, pit on the rear of the head (postgenal fossa or pit);
- pgc*, postgenal scar (cicatrix) or scars;
- poc*, postocellar tubercle;
- pot*, posterior occipital tubercle;
- prs*, parocular groove (sulcus);
- r*, ridge on rear of head (postgenal fastigium or ridge);
- soc*, superior ocular scar (cicatrix) or scars;
- tr*, transverse posterior ridge of vertex.

Unless otherwise stated, all the figures on these three plates have been drawn with the camera lucida, drawing at stage level. with Zeiss compensating ocular no. 2. objective A (lower lens *off*), and their average magnification on the plates is 8.0. Details were added by freehand, using a Zeiss binocular with paired oculars 4 and paired objectives F 55.

All the drawings by the writer.

Plate XIII

Figs. 1 to 7.—*Epigomphus subsimilis* new species. Turrúcares, Costa Rica, August 14, 1909, type ♂ and allotype ♀. 1 to 3 and 6—left profile, dorsal, ventral and caudal views respectively of the apex of the ♂ abdomen. 4—Genitalia of the second abdominal segment ♂, extruded, left profile view; objective A here with lower lens *on* × 12.6; *hp*, posterior hamule; *lig*, ligula (Schmidt) or sheath of the penis; *pn*, penis; *vp*, vesicle of the penis; *pn* 2, morphologically dorsal surface of the apex of the penis; *ha*, apex of anterior hamule (concealed within the posterior hamules) and *lig.p*, apex of lateral process of ligula, drawn free hand and on a larger scale. Figs. 5 and 7.—Dorsal and caudal views respectively of head of female.

³³These three, pit, ridge and tubercle, are probably homologous; see under *E. subobtus*, *antea*, pages 348–9.

Figs. 8 to 10.—*E. quadracies*, Rio Chirripo, C. R. 8.—Dorsal view of apex of abdomen of ♂ of July 26, 1915. 9 to 10.—Dorsal and caudal views respectively of head of ♀ of July 25, 1915.

Plate XIV

Figs. 11 to 14, 18 to 22.—*E. tumefactus*, Florida Road, June 3, 1909, ♂ and ♀; in figs. 11–14, 18–19, the proximal end is upper in every case. 11 and 12.—Right third femora, anterior surface, ♀ and ♂ respectively. 13 and 14.—Right third tibiae, anterior surface, ♀ and ♂ respectively. 18 and 19.—Right third tarsi, anterior surface, ♀ and ♂ respectively. 20.—Dorsal view of apex of ♂ abdomen; *d*, denticles of inferior appendage. 21 and 22.—Dorsal and caudal views respectively of head of female; the postgenal scars *pgc*, of Biolley's female have been added to fig. 22.

Figs. 15 to 17.—*E. subobtusus*. 15.—Dorsal view of apex of abdomen of ♂, Juan Viñas, C. R.; the superior appendages of this individual are not as widely distended as they probably are when mating. 16 and 17.—Dorsal and caudal views respectively of head of female from south of Aguacaliente, C. R.

Plate XV

Figs. 23 to 26.—*E. verticicornis*, Tuis, Costa Rica, type ♂ and allotype ♀. 23.—Inner dorsal oblique view of left superior appendages and left half of inferior appendage ♂; *rs*, base of right superior appendage; *x'*, "downwardly directed spine" of the inner (mesal) surface of the left superior appendage; *y*, "forwardly curved spine" of the dorsal surface of the basal part of the inferior appendage. 24.—Dorsal view of apex of abdomen of ♂, appendages somewhat distorted; *y*, as in fig. 23. 25 and 26.—Dorsal and caudal views respectively of head of female; *x*, linear depressions mentioned in text, page 340.

Figs. 27 to 30.—*E. armatus*. 27 and 28.—Ventral and left profile views respectively of apex of abdomen of ♂, copied from Dr. Ris's figures 92 and 93; left superior appendage removed in figure 28; magnification not stated. 29 and 30.—Dorsal and caudal views respectively of the head of ♀ from the Florida Road of June 5, 1909; the superior ocular cicatrices (*soc*) from the female of June 3, have been added to fig. 29.

CALVERT—COSTA RICAN EPIGOMPHUS



